A new species of soldier crab, *Mictyris occidentalis* (Crustacea: Decapoda: Brachyura: Mictyridae) from Western Australia, with congener comparisons

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Abstract

Mictyris occidentalis, a new species of mictyrid crab (commonly known as soldier crab), is described from Western Australia. Diagnostic features include the macroscopically granular carapace; prominent granular ridges running posteriorly from the antero-lateral spines; front with broadly curved lateral lobes; rounded and projecting shape of the carapace posterior border and distinctly curved and setose dactyls on the 4th pair of walking legs. The new species combines characteristics of congeners *M. longicarpus* Latreille, 1806 and *M. brevidactylus* Stimpson, 1858 with which it is compared biometrically. *M. occidentalis* is the only *Mictyris* species extant from Shark Bay to Broome in Western Australia and is likely to be endemic. The taxonomic history of *Mictyris* species is summarised, and recognition of *M. brevidactylus* as a separate Asian species/ species complex and *M. longicarpus* as endemic to the eastern coast of Australia is supported. A key to the described species of *Mictyris* is provided.

Keywords: Intertidal crab, Mictyridae, *Mictyris occidentalis*, new species, soldier crab, taxonomy, endemic, Western Australia.

Introduction

Soldier crabs (*Mictyris* spp.) are well-known inhabitants of tidal flats and beaches in the central Indo-west Pacific region, highly visible in large roving "armies" of several hundred small, round blue crabs emerging during low tide. They are also distinctive in their unique ability among the Brachyura to walk (or run) forwards, the presentation of the cheliped carpus in a vertical plane (similar to a praying mantis), and their habit of rapidly burrowing into the substrate in a corkscrew motion. Besides the *Mictyris* species, the common name "soldier crab" has also been applied to other crustaceans such as hermit crabs (the European *Parurus bernhardus* and the Caribbean *Coenobita clypteatus*), the ocypode crab *Dotilla myctiroides* from South-east Asia and, occasionally, the Christmas Island Red Crab, *Gecarcoidea natalis*, however, the term "soldier crab" is most commonly applied to species of *Mictyris*.

A brief review of the taxonomic history of *Mictyris* and its inherent problems is provided as background for the description of the new species.

This paper describes *Mictyris occidentalis*, a new species from the monotypic Family Mictyridae Dana, 1851, consistent in morphological characteristics across a distribution recorded thus far from Monkey Mia, Shark Bay to One Armed Point, near Cape Leveque on the mainland coast of Western Australia (Fig. 1). As such, it is a contribution towards clarifying a part of the complex of species referred to *Mictyris longicarpus* (Davie 1982, 1985, 2002). Habitat, behaviour and distribution of *M. occidentalis* also are described briefly.

The new species is morphologically and biometrically compared with two other *Mictyris* species, *M. longicarpus* and *M. brevidactylus*. All three species of *Mictyris* examined in this study were previously assigned by McNeill (1926) to either *M. longicarpus*, including *Mictyris* collected from the Western Australian coast (*i.e.*, the *M. occidentalis* of this study), or in the case of *M. brevidactylus* Stimpson, 1858, to a variety of *M. longicarpus* (*viz. M. longicarpus* var. *brevidactylus*) restricted to South-east Asia. To determine clearly whether there is one species with varieties (as McNeill suggested), or there are three separate species in this congener group, it was necessary to undertake detailed comparisons between the three forms.

The paper also provides a key to help differentiate between the five species of *Mictyris* described to date.

Taxonomic history

While the Family Mictyridae Dana, 1851 has its own convoluted history (*e.g.*, Crane 1975 refers "Myctyris"[*sic*] to the Ocypodidae; Jones 2004 similarly referred *Mictyris* that occurred in Withnell Bay, Western Australia to the Ocypodidae), this paper is concerned not with the history and status of the Family but only with *Mictyris* itself as a context to the identification of a new species. However, this section on taxonomic history does not attempt an exhaustive treatment of synonymies on species of *Mictyris*, which can be found in the literature, but rather focuses on the problems in taxonomy resulting in *M. occidentalis* being originally assigned to

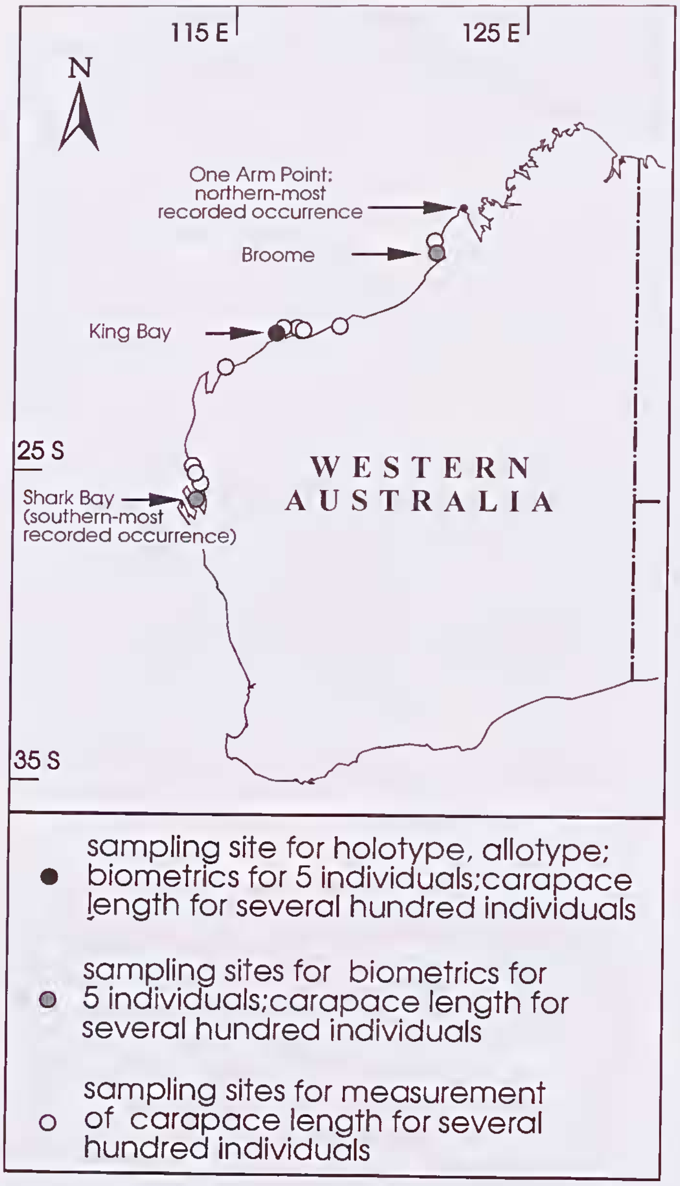

Figure 1. Map of Western Australia showing location and types of sampling sites for *Mictyris occidentalis*.

M. longicarpus, and in *M. brevidactylus* from South-east Asia being confused with *M. longicarpus* even today, more than 200 years since the holotype was first described.

The taxonomic history of *Mictyris* is similar to that of a multitude of taxa which were originally described in the early 19th Century from collections made on European exploratory voyages to the Indian-Pacific region. Early diagnoses were often very brief due to the large number of organisms collected and there was a tendency to place superficially similar specimens into existing groups rather than create new taxa. Frequently, type locations from early voyages were regional (*e.g.*, "east Indian Ocean"), rather than site-specific, or sometimes were incorrectly recorded, and often specimens were described at a later date, not by the collector but by another worker, usually a museum taxonomist. Consequently, over time, many taxa have undergone numerous revisions and have been re-assigned by various authors, as species differences have become apparent. Besides imprecise distributions, other problems included limited access to literature in foreign languages, particularly early references, and the creation of synonymies. The misspelling of species names in the literature also added to the taxonomic confusion of some groups, including the Mictyridae (Alcock 1900).

The genus *Mictyris* with its holotype *Mictyris longicarpus* and the nebulous type locality of "Oceano Indiae orientalis", was originally described by Latreille in 1806 from a collection in the Paris Museum. Latreille was not the collector, hence the vagueness of the type locality, a problem which still has repercussions for researchers today. To Latreille's credit, efforts were made to clarify the type location and later the locality was amended to " l'Océan australasien" (Latreille 1829). The species *Mictyris longicarpus* was referred to by subsequent authors under numerous misspellings, *e.g.*, "*Myctiris longicarpis*" (Milne Edwards 1837), before being corrected to the original name by Alcock (1900) who also gave a more detailed description of the genus. Dana (1851) elevated the genus to family status, a move supported by Kemp (1919), McNeill (1926), and most of the recent brachyuran catalogues (*e.g.*, Davie 2002). A second species of *Mictyris* in Australia, *M. platycheles*, was described by Milne Edwards (1852) from 'Port Western' (Western Port Bay), Victoria with a distribution from Moreton Bay, Queensland to the north coast of Tasmania. The *nomen nudum Myctiris subverrucatus* was given to a specimen from Tasmania by White in 1847 but since has been assigned to the synonymy of *M. platycheles* along with the provisional name *Myctiris prostoma* suggested by Stimpson in 1907 (McNeill, 1926). De Haan (1835) published the name *Mictyris deflexifrons* (recognised now as a *nomen nudum*) for specimens from Japan (which are now assigned to *M. brevidactylus*, see below)

The next important stage in the history of *Mictyris* taxonomy was the work of Stimpson (1858) who described very briefly, but did not illustrate, *Mictyris brevidactylus* from the southern coast of China and the islands of "Loo Choo" (Ryukyu Islands, Japan), and definitively established that the South-east Asian *Mictyris* did not belong to *M. longicarpus*. Unfortunately, the types of *M. brevidactylus* were lost in a fire at the Chicago Academy of Sciences in 1871 and William Stimpson died in 1872 without publishing a full description and figure of the new species. In 1907, Dr Mary J. Rathbun, who, as assistant curator of the United States National Museum, was familiar with Stimpson's concept of *M. brevidactylus*, published a posthumous paper by Stimpson which described and contained figures of *M. brevidactylus*, and gave its distribution from Hong Kong, South China Sea, to the Ryukyu Islands, southern Japan (Stimpson 1907). However, this paper (Stimpson 1907) did not eliminate the confusion over the misuse of the name "*M. longicarpus*" in South-east Asia and Japan. Adding to the taxonomic confusion, De Man (1887) and Tesch (1918) regarded *M. brevidactylus* Stimpson to be synonymous with *M. longicarpus*, although McNeill (1926) argued that these workers were not in possession of specimens of true *M. longicarpus* from eastern Australia for proper comparison, unlike Stimpson who had collected material from Port Jackson and Botany Bay, in New South Wales (NSW).

McNeill (1926), in a significant revision of the Mictyridae, recognised three species and one variety of soldier crab in the Indo-Pacific and Australian regions. These were: *Mictyris longicarpus* Latreille, 1806; *Mictyris platycheles*" H. Milne Edwards, 1852; *Mictyris livingstonei* McNeill, 1926 (type locality at Trial Bay with a distribution from Cooktown, Queensland (Qld.) to Trial Bay, northern NSW), and *Mictyris longicarpus* var. *brevidactylus* (Stimpson). McNeill did not give a rationale for changing the status of *M. brevidactylus*, although he did suggest that future workers would find local "definite racial forms" within the distributional area of the variety. In addition, with regard to the identity of true *M. longicarpus*, McNeill (1926) provided a detailed argument for the type location of Latreille's *M. longicarpus* as Port Jackson (NSW), on the east coast of Australia. McNeill set the distribution of *M. longicarpus* (in Australia) as being from the lower NSW coast northwards, across the northern part of Australia and along the coast of Western Australia to Perth in southwestern Australia, and stated that soldier crabs from the Philippine Islands and northwards to the China Sea should be referred to *M. longicarpus* var. *brevidactylus*. The record from Perth (Miers 1884), on which McNeill (1926) rests the southwestern-most occurrence of *M. longicarpus* in Western Australia, is unlikely to be correct as there are no other records of *Mictyris* further south than Shark Bay along the Western Australian mainland coast. [I have not found *Mictyris* south of Shark Bay on the Western Australian mainland coast in extensive surveys of appropriate sandy tidal flat habitats in the estuaries from Kalbarri to Perth between 1997 and 2007].

Of particular relevance to this paper was McNeill's treatment of a series of specimens from the general locality "North West Australia" including Cygnet Bay north of Broome in Western Australia. Despite observing that the "greatest divergence from the typical form" occurred in this series, McNeill (1926) conservatively assigned the Western Australian populations of soldier crabs to *M. longicarpus*. The characters which McNeill listed for "North West Australia" are consistent with *M. occidentalis*, although McNeill does not mention the unique projection of the carapace posterior border or the gonopod morphology (as described in this paper). As such, the taxon "*M. longicarpus* (*pro parte*)" referred to in the synonymy of this paper (see below) refers to those *Mictyris* crabs from Western Australian that were assigned to *M. longicarpus* by McNeill (1926).

Notwithstanding the revisions by McNeill (1926), later workers, especially in the Japanese and South-east Asian regions, still held to Latreille's initial broad type locality (*i.e., M. longicarpus* occurred everywhere, from Japan to Australia). Sakai (1976), for instance, stated that Japanese crab fauna contained a single *Mictyris* species, *M. longicarpus,* and agreed with Tesch (1918) that *M. brevidactylus* was synonymous with *M. longicarpus*. At that time, Japanese carcinologists referred Japanese specimens to *M. longicarpus* as they had not accessed McNeill's paper which limited the distribution of true *M. longicarpus* to Australia (Takeda 1978). Takeda (1978), citing McNeill's 1926 paper, compared "*M. longicarpus*" from the Ryuku Islands with *M. longicarpus* from New South Wales and regarded them as "specifically distinct". Currently, some workers accept *Mictyris brevidactylus* as a synonym or just a variety of *M. longicarpus* (*e.g.*, Kawaguchi 2002), while others, notably most Australian, Japanese, Chinese and South-east Asian researchers (*e.g.*, Shih & Liao, 1998; Takeda, 2005) accept the designation of Stimpson (1858, 1907).

Davie (1982, 1985, 2002) suggested that *Mictyris* in Australia is a "complex" of five species: three from eastern Australia have been described (*M. longicarpus* Latreille, 1806, *M. platycheles* H Milne Edwards, 1852 and *M. livingstonei* McNeill, 1926); one from the Northern Territory remains undescribed; and the fifth from Western Australia is the subject of this paper.

This present study strongly supports recognition of full species status for *M. brevidactylus* Stimpson, 1858 and, following Davie (2002), *M. longicarpus* (*sensu stricto*) as being restricted to eastern Australia. Other records of *M. longicarpus* from elsewhere in Australia and the Indo-west Pacific Ocean are either misidentifications or are of undescribed species.

Materials, methods and terminology

Materials examined:

***Abbreviations*:**

♂ = male, ♀ = female, J = juvenile, ovig = ovigerous, AM = Australian Museum, WAM = Western Australian Museum, VCSRG = V & C Semeniuk Research Group, max = maximum, CL = carapace length

***Material for comparison and biometric study*:**

Mictyris occidentalis: 4 ♂♂ (CL 12.90–12.73 mm) WAM C39422, King Bay, Dampier Archipelago, WA, 2004; 5 ♂♂ (CL 14.96–13.36 mm) WAM C39423, Broome WA, 2004; 5 ♂♂ (CL 12.95–10.52 mm) WAM C39424 Monkey Mia, Shark Bay, WA, 2004

Mictyris brevidactylus: 3 ♂♂ (CL 12.01–9.07 mm), 3 ♀♀ (CL 11.32–8.47 mm) AM 5750 Subig Bay, north Philippine Islands, 1908; 4 ♂♂ (CL 15.25–11.14 mm) AM P73642 Starfish Bay, New Territories, Hong Kong, 2006

Mictyris longicarpus: 7 ♂♂ (CL 19.58–11.23), 3 ♀♀ (CL 15.15–13.12) WAM C13323 Cape Ferguson, Townsville, Queensland, Australia, 1982

Material from Australian localities:

M. occidentalis in the VCSRG collection: 4 ♂♂ (CL 12.90–12.73 mm), 2 non ovig ♀♀ (CL 10.6–9.2 mm), 1 ovig ♀ (CL 8.80 mm), 32 JJ (CL 6.00–1.20 mm) VCSRG 80804 Coconut Well, WA, 2004; 62 ♂♂ (CL 15.10–7.30 mm), 3 non ovig ♀♀ (CL 10.40–9.20 mm), 92 JJ (CL 4.70–1.50 mm) VCSRG 70804, Broome, WA, 2004; ♀♀ VCSRG 110294 Port Smith, WA, 1994; 255 ♂♂ (CL 13.90–7.10 mm), 192 non ovig ♀♀ (CL 10.50–7.10 mm), 1 ovig ♀ (CL 9.40 mm), 68 JJ (CL 6.50–1.40 mm) VCSRG 120704COSS, Settlers Beach, Cossack, WA, 2004; 2 ♂♂ (CL 7.80–7.70 mm), 1 non ovig ♀♀ (CL 6.70 mm), 179 JJ (CL 5.80–1.40 mm) VCSRG 140704 Point Sampson, Cape Lambert, WA, 2004; 37 ♂♂ (CL 12.90–7.00 mm), 5 non ovig ♀♀ (CL 10.90–7.00 mm), 5 ovig ♀♀ (CL 8.90–7.00 mm), 272 JJ (CL 5.70–1.50 mm) VCSRG 150704 Hearson Cove, Dampier Archipelago, WA, 2004; 152 JJ (CL 6.40–1.50 mm), VCSRG 120704WB Withnell Bay, Dampier Archipelago, WA, 2004; 295 ♂♂ (CL 13.90–7.00 mm), 208 non ovig ♀♀ (CL 10.90–7.00 mm), 5 ovig ♀♀ (CL 9.40–7.00 mm), 527 JJ (CL 6.90–1.00 mm) VCSRG-DA, Dampier Archipelago, WA, 2001–2003; 2 ♂♂ (CL 8.20–7.50 mm), 5 ovig ♀♀ (CL 9.90–7.50 mm), 4 JJ (CL 3.90–3.20 mm) VCSRG 110704ONS Onslow, WA; 42 ♂♂ (CL 15.80–7.30 mm), 31 non ovig ♀♀ (CL 12.50–8.60 mm), 10 ovig ♀♀ (CL 9.90–7.50 mm), 467 JJ (CL 5.60–1.20 mm) VCSRG 110704CARN Carnarvon, WA; 23 ♂♂ (CL 15.40–7.00 mm), 32 ♀♀ (CL 12.20–6.80 mm), 4 JJ (CL 6.50–5.50 mm) VCSRG 100704MM Monkey Mia, Shark Bay, WA; 3,995 ♂♂, ♀♀, JJ (CL 13.9–1.0 mm) VCSRG 19802003 King Bay, Dampier Archipelago, WA, 1980–2003.

M. occidentalis in the WAM Collection: 1 ♂ (CL 13.09 mm) C39414 One Armed Point, NW Kimberley, WA; 1 ♂ (CL 14.15 mm) C13294 Gnamagun (Lombardine Mission) WA, 1982; 2 ♀♀ WAM C12970, 1980 & C16995, 1978, Barrett Creek NW Broome, WA; ♂♂, ♀♀, JJ (max CL 15 mm) C12979, C12940, C12934, C39405 Broome, WA, 1980; ♂♂, ♀♀, JJ (max CL 11.71 mm) C8037, C39398, C39399 & C39415 Mundabullangana, near Port Hedland, WA, 1960; ♂♂ C13009 & C13010 Mko Bay, Cape Lambert, WA, 1979; 1 ♂ (CL 12.14 mm) C39408 Legendre Is. Dampier Archipelago WA 1962; ♂♂ C25898, C26685, C29204 Dampier Archipelago, WA, 1998–99; ♂♂ (max CL 15.27 mm), C11871, C23036, C23354, C13001-05, C38788-90, C39390, Ningaloo/Exmouth Gulf region WA, 1974–95; ♂♂ (max CL 14.00 mm) C5689, C22231, C39402, C39409-10, Carnarvon region, WA, 1939–76; 1 ♂ (CL 15.53 mm) Faure Is., Shark Bay, WA, 1958; ♀♀ ♂♂ (max CL 17.49 mm) C8038, Monkey Mia, Shark Bay, WA, 1960.

M. longicarpus in the WAM Collection: 1 ♀ (CL 13.27 mm) 1 C39392, Sandfly Creek, MacKay, QLD, 1983; 1 ♂ C8039 Townsville, QLD 1961; 1 ovig ♀ C13327 Townsville, QLD, 1982; 1 ♂ C13348, Townsville, QLD, 1982

M. livingstonei in the WAM Collection: 1 J, C39401, Sandfly Creek, MacKay, QLD, 1983; 1 ♂ C39416, Andergrove, QLD; 1 ♂ C39418 Yorky's Knob, Cairns, QLD, 1983

M. platycheles in the WAM Collection: 1 ♂ C39396, Altona Pier, VIC, 1965

Mictyris sp. in the WAM Collection: 4 ♂♂ (CL 15.38–12.01 mm), 2 ♀♀ (CL 11.54–11.05 mm), 19116 NW of Unwins Island, north Kimberley, WA, 1988 (*Mictyris longicarpus* is on the Museum label); 1 J C39389 Lee Point, Darwin, NT; 1 ♂ (CL 12.00 mm) C39395 West Woody Island Creek Gove, NT

***Material from non-Australian localities*:**

Mictyris brevidactylus in the WAM Collection: ♂♂ C39406, C39412, C39413 Hong Kong

Taxonomic work and morphological descriptions and comparisons in this study were based on: (1) data from several hundred specimens collected and examined across a large latitudinal gradient in Western Australia (25° S to 16° S); and (2) a particular focus on obtaining correctly identified specimens of *M. brevidactylus* and *M. longicarpus* for accurate taxonomic comparison of characters.

To determine which soldier crab species were extant in Western Australia, *circa* 1000 specimens were collected from populations in 18 sub-tropical to tropical coastal sites for morphological and biometric studies (Fig. 1 and Table 1, all co-ordinates in WGS84 system).

Table 1

Broome to Shark Bay regional study collection sites from localities in WA

Region	Locality/Site	Latitude & Longitude
Broome	Coconut Well	17° 49' 16.37" S 122° 12' 44.78" E
	Riddell Beach	17° 59' 05.15" S 122° 11' 28.02" E
	Broome Town high tide	17° 58' 02.47" S 122° 14' 16.34" E
	Broome Town mid-tide	17° 58' 02.47" S 122° 14' 16.34"E
Port Hedland	Port Hedland spoil bank	20° 18' 26.80" S 118° 35' 28.30" E
	6 Mile Creek	20° 19' 24.90" S 118° 39' 52.56" E
	12 Mile Creek	20° 20' 09.60" S 118° 40' 20.89" E
Cape Lambert	Settlers Beach (near Cossack)	20° 40' 03.20" S 117° 14' 40.24" E
	Point Samson	20° 37' 47.46" S 117° 11' 51.04" E
Dampier Archipelago	Hearson Cove landward of *Avicennia*	20° 37' 37.63" S 116° 47' 53.11" E
	Hearson Cove sand flat	20° 37' 42.14" S 116° 47' 51.41" E
	Withnell Bay	20° 34' 26.65" S 116° 47' 48.83" E
	King Bay-King Bay Shoal	20° 38' 0.8.56" S 116° 45' 25.48" E
	King Bay-KB12	20° 38' 10.38" S 116° 45' 28.87" E
Ashburton River Delta	Onslow	21° 38' 52.28" S 115° 07' 50.74" E
Gascoyne River Delta	One Tree Road	24° 51' 43.40" S 113° 37' 43.90" E
	Mile Jetty	24° 54' 09.85" S 113° 40' 01.97" E
	Mile Jetty West	24° 54' 09.85" S 113° 40' 01.97" E
Shark Bay	Carnarvon racecourse	24° 54' 15.1m4" S 113° 40' 19.18" E
	Monkey Mia	25° 47' 36.44" S 113° 43' 18.05" E

These collection sites ranged from Monkey Mia, Shark Bay in the south to Coconut Well (north of Broome) in the north-west of Western Australia across a wide latitudinal range of 9°, a distance of *circa* 1000 km. Specimens examined were morphologically consistent throughout the study area signifying that only one species was present. Five adult male specimens from three sites (Monkey Mia, King Bay and Broome) selected to cover the coastal range, were then compared with five *M. longicarpus* and three *M. brevidactylus* adult male specimens obtained from the Western Australian Museum (WAM) and the Australian Museum (AM), respectively. The WAM holding of *M. longicarpus* was collected from Townsville in Queensland on the east coast of Australia and accorded with Latreille's type description. This last point is particularly important because WAM specimens examined in this study, which were collected from Western Australian localities and attributed to *M. longicarpus*, did not correspond to Latreille's description of the holotype of *M. longicarpus*.

Similarly, it was considered important to obtain correctly identified specimens of *M. brevidactylus* for comparison. As previously mentioned, Stimpson's holotype of *M. brevidactylus* was destroyed by fire in 1871, however, the Australian Museum provided specimens of *M. brevidactylus* from Subig Bay, Luzon in the northern Philippine Islands. These were identified by Rathbun using Stimpson's identification criteria and included the adult male specimen which McNeill (1926) described as *M. longicarpus* var. *brevidactylus* Stimpson, in his revision of the Family Mictyridae.

Thirty characters (Table 2) which were considered useful diagnostically were selected for the biometric study as a means of species determination, and these were measured to the nearest 0.01 mm with a digital vernier caliper (DSE Model Q1382). Figures 2B, 2C, 2D & 2E show the location of anatomical features used in biometrics in this paper. Measurements of features (*e.g.*, leg, eye, *etc.*) were obtained on the right side of the crab

Table 2

Diagnostic characters and other abbreviations used in this paper

Character	Description	Abbreviation
Abdominal segment 1	straight line length of 1st abdominal segment measured along the mid-line	AS1L
Abdominal segment 6	length of 6th abdominal segment measured along the mid-line	AS6L
Abdominal segment 7	length of 7th abdominal segment measured along the mid-line	AS7L
Antero-lateral spines interspace	distance between inner bases of antero-lateral spines	ALSI
Body Height	Vertical distance between top of carapace and lowest point on abdomen	BH
Carapace anterior to posterior	length between front and edge of posterior border of carapace (not including setae)	CL
Carapace lateral dimensions	distance between widest point of branchial regions	CW
Cheliped carpus anterior to posterior	straight line distance between top of wrist to distal end, along outer edge	CHCL
Cheliped carpus distal edge	length of distal edge of wrist	CHCW
Cheliped dactyl	length of moveable finger	CHDL
Cheliped palm lower margin	length of palm on lower margin	CHPLlm
Cheliped palm upper margin	length of palm on upper margin	CHPLum
Cheliped pollex	length of immoveable finger	CHPOL
Cheliped palm	depth of palm	CHPW
Cornea	distance from top of eye to start of peduncle	COL
Cornea plus peduncle	distance from tip of cornea to base of peduncle	COL+PED
Eye interspace	Distance between outer extremities of eyes	EI
Front lateral dimensions	horizontal distance across top of frontal lobe	FW
Front vertical dimensions	distance from the median point of the front, level with the eyes, to the point of the median lobe	FL
Gastric region lateral dimensions	width of gastric region	GW
Median carapace dimensions	width of middle part of carapace (mid-branchial region)	MCW
Posterior border setae	length of setae lining posterior border	PBH
Posterior border lateral margin	distance in a straight line from distal corner of carapace border to beginning of curve around ischium of 4th walking leg	PBL
Posterior border caudal margin	width of rear carapace border from corner to corner	PBW
3rd maxilliped	total length of 3rd maxilliped from top of merus to bottom of ischium	3MTL
3rd maxilliped merus	central length of merus	3MML
3rd maxilliped ischium naked surface	central length of bare ischium surface	3MILns
3rd walking leg merus	length of part measured centrally	3WLML
4th walking leg dactyl	length of part measured centrally	4WLDL
4th walking leg propodus	length of part measured centrally	4WLPL
4th walking leg merus	length of part measured centrally	4WLML

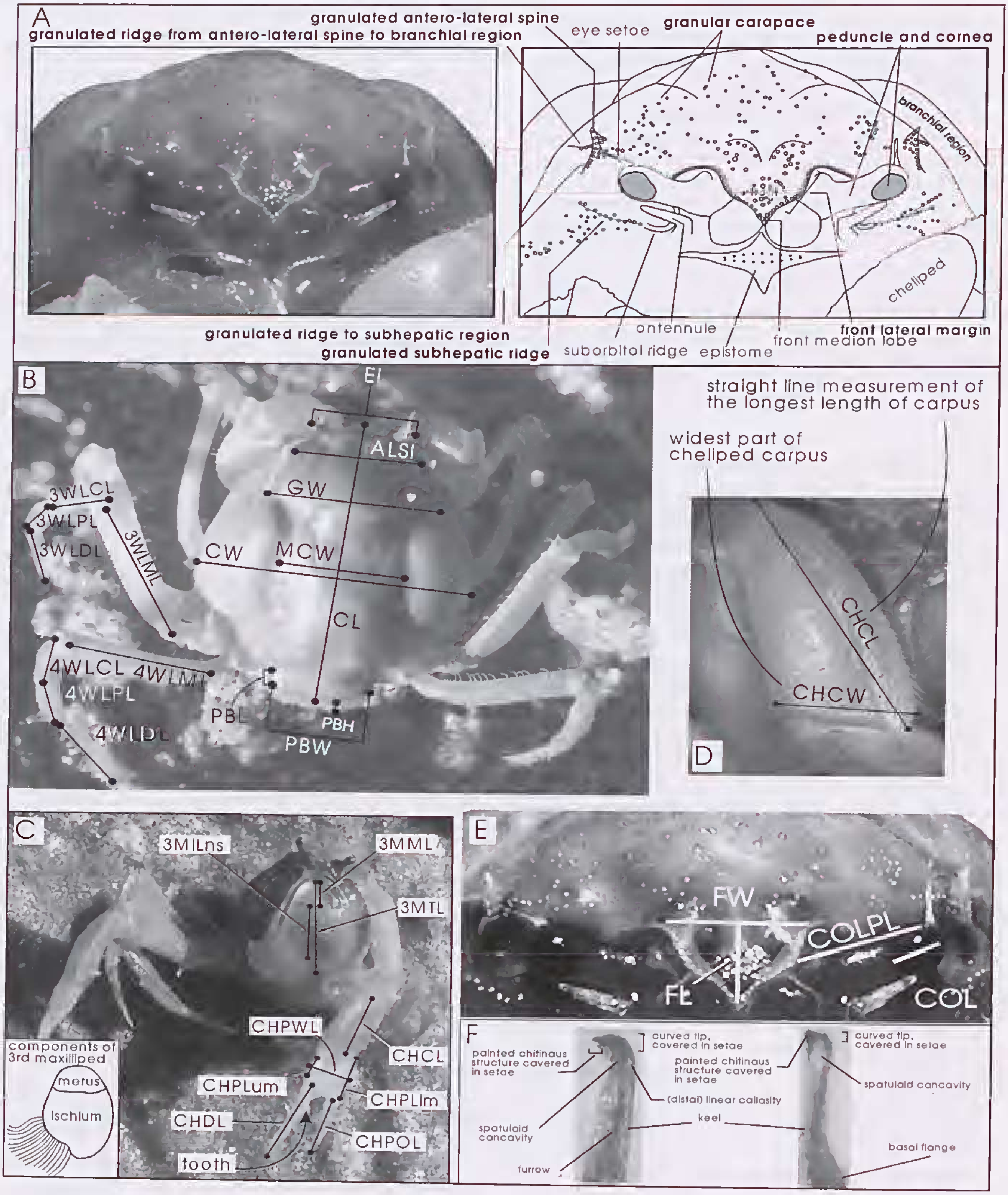

Figure 2. Skeletal anatomy of *Mictyris* and a key to those features used in biometrics in this paper. A. Key features evident in the anterior view; those annotated in bold print are diagnostic for *Mictyris occidentalis*. B. Dorsal view showing location of anatomical features used in biometrics in this paper. C. Oblique dorsal view showing location of anatomical features used in biometrics in this paper. D. Close-up of cheliped to illustrate location of the straight line measurement used for determination of carpus length and width. E. Front view showing location of anatomical features used in biometrics in this paper. F. Anatomical features of the gonopods. Key to the acronyms is presented in Table 2.

Table 3
Ratios of morphological characters used in this paper

Ratios following McNeill (1926)	Ratios devised for this paper
ALSI:PBW	CHCL:CHCW
CHPW:CHPLlm	CHCL:ALSI
CHDL:CHCL	CHPOL:CHPLlm
CHPOL:CHCL	CL:BH
CHPW:CHPLlm	4WLML:PBL
CHPW:CHPOL	4WLML:4WLDL
CL:CW	
COL:COL + PED	
EI:PBW	
EI:MCW	
FW:FL	
3MML:3MILns	
3MTL:ALSI	
3MTL:CHPLum + CHDL	

body, unless the feature was missing, in which case, the left side was utilised. Averages were taken of the individual measurements for each group of crabs and these data were used to determine the character ratios employed in the comparisons.

The terminology used here follows McNeill (1926), particularly in the terms for the cheliped where the wrist = carpus, palm = manus, immoveable finger = pollex and moveable finger = dactyl. Abbreviations employed in this paper are shown in Table 2.

Use of ratios of particular morphological features largely follow McNeill (1926), particularly for the ratios of CW:CL, all the 3rd maxilliped ratios, ALSI:PBW, CHPW:CHPLlm, and FW:FL. However, other ratios have been devised for this paper to highlight diagnostic characteristics of *M. occidentalis* (Table 3).

Taxonomy

MICTYRIDAE Dana, 1851

***Mictyris* Latrielle, 1806**

Type species: *Mictyris longicarpus* Latreille, 1806

***Mictyris occidentalis, sp. nov.* (Figures 2, 3)**

***Mictyris longicarpus* (*pro parte*). - McNeill 1926: page 109 ("north west coast" material)**

Material examined

Holotype: male (CL 12.46 mm, CW 10.32 mm) WAM C39420, King Bay, Dampier Archipelago, Western Australia, 20° 38' 16" S, 116° 45' 50" E (WGS84), coll. J. Unno, 24 Apr 2003.

Allotype: female (CL 10.06 mm, CW 8.15 mm) WAM C39421, King Bay, Dampier Archipelago, Western Australia, Lat. 20° 38' 16" S Long. 116° 45' 50" E (WGS84), coll. J. Unno, 24 Apr 2003

Diagnosis

M. occidentalis is distinguished from other *Mictyris* species by a visibly granular carapace, especially on the antero-lateral spines and associated ridges, and a convexly rounded posterior border, viewed dorsally, projecting beyond the abdomen. The chelipeds are strongly granulated with well-defined granular ridges on the palm and fingers, and the dactyls of the fourth walking legs are distinctly curved.

Description of male holotype

Body: Sub-globular (Fig. 3A), width between widest part of branchial regions less than length from front to posterior border of carapace (CL:CW= 1.21:1); body extends to slightly forward of bases of antero-lateral spines. Branchial regions inflated and projecting over lower edges of carapace at bases of ambulatory limbs. Posterior border of carapace (Fig. 3C) truncated and produced beyond curve of abdomen, slightly convexly curved outward along its width which is slightly less than the interspace between the antero-lateral spines (ASLI:PBW=1.22:1); lateral margins are rounded and length of sides are one fifth the width of border; a fringe of long setae lines the border margin and sides with the length of setae (PBH) being approximately three-quarters of the length of the sides (PBL).

Carapace: Visibly granular and not smooth to touch (Figs. 2B & 3A). Gastric and branchial regional grooves well-defined. Branchial regions visibly granular with closely-set granules covering branchial region and forming rugae on the posterior halves. Median areas with groups of macroscopic granules particularly on the gastric region near the antero-lateral spines and on the cardiac mound which also has several rounded tubercules; two chitinised stigmata on central posterior border of gastric region; two short, longitudinal grooves adjacent to each branchial region with a pair of small tubercules in the centre of the median area; two small pits at base of cardiac mounds each adjacent to bases of 4th walking legs. Sub-hepatic regions visible from above; strong granular ridge running along front of sub-hepatic regions downwards to oblate Milne Edwards openings above the cheliped basis on either side; macroscopic strong granular ridges extend inwards from sub orbital border, diminishing to microscopic granules below antero-lateral spines; antero-lateral spines (Fig. 2A), prominent, obtusely pointed, recurved, granular at bases and on anterior faces; directed obliquely upwards and outwards; a macroscopic, strongly granular ridge extends posteriorly from base of each antero-lateral spine to branchial region and another short, sparsely granular ridge extends downwards towards sub-hepatic region from base of antero-lateral spine; interspace between antero-lateral spines is almost equal the distance between the outside of the eyes, 1.22 times the width of the posterior border and almost equal the width of the space between the mid branchial regions. Front is vertical (Figs 2A and 3B), broad and channeled; length is four fifths of the width (Fig. 2E); lateral lobes broadly conversely curved, median lobe obtusely pointed and sides obversely curved; margin of front is carinated and granular; clusters of macroscopic granules occur on the epigastric ridges and the center of the median lobe.

Eyes: Smaller than in the type species (*M. longicarpus*); the space between the outside of the eyes (Fig. 2B) slightly greater than the width of the posterior border (EI:PBW = 1.14:1); cornea tipped with

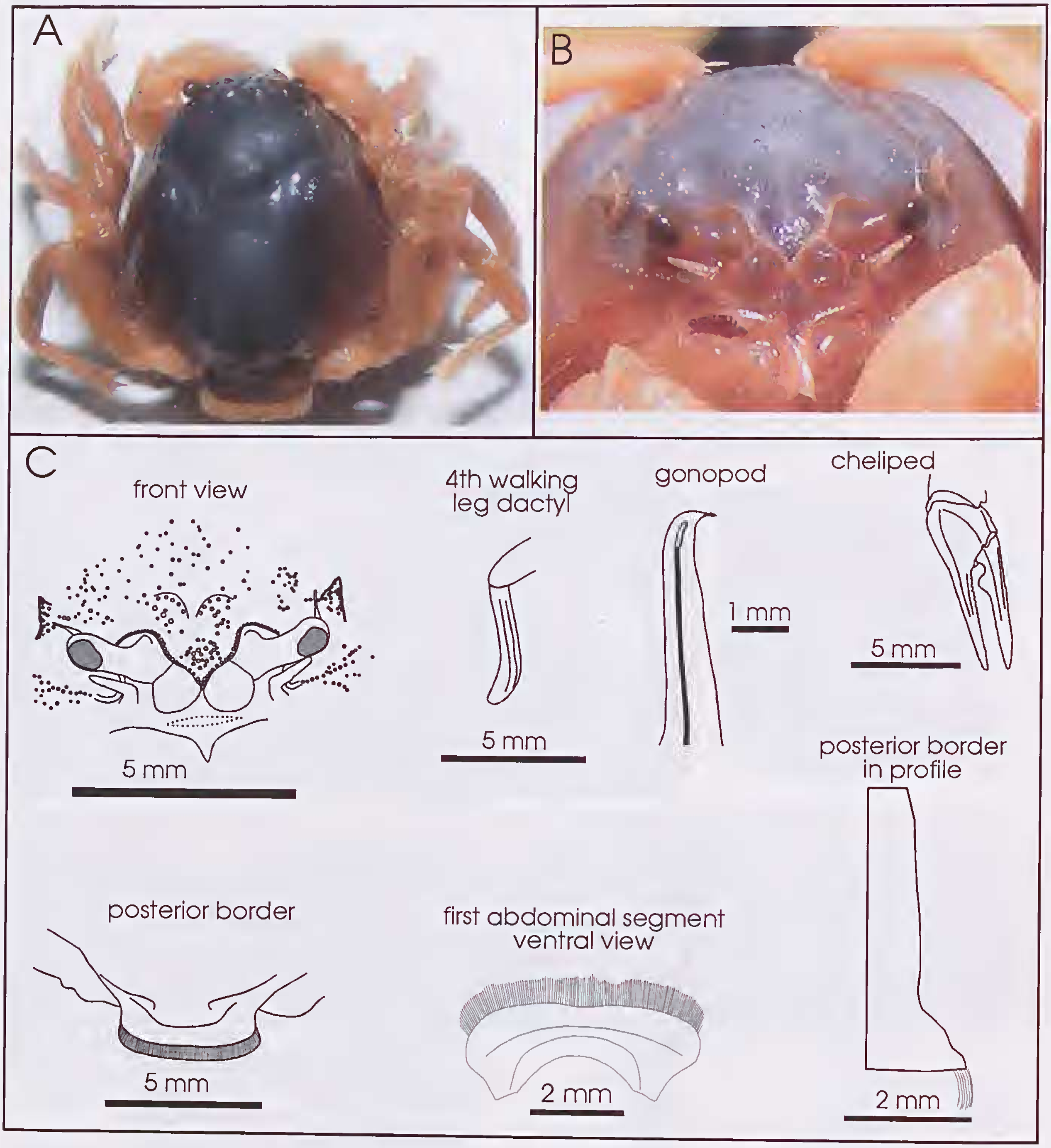

Figure 3. Anatomical features of the holotype and paratypes of *Mictyris occidentalis*. A. Dorsal view of the holotype (KB5) showing inflated nature of the carapace, the posterior border and its fringe of setae, and the curved dactyl of the 4th walking leg. B. Front of the paratype (KB1) showing granulated anterior part of carapace, the carinated, granular margin of the front, and the granulated antero-lateral spine. C. Drawing of key features of *M. occidentalis* using paratypes. The illustrations show the nature of the granulated and carinated front margin; the granulated antero-lateral spines, and the granulated ridge from the antero-lateral spines to the branchial region; the curved dactyl of the 4th walking leg; the geometry of the gonopod; the features of the cheliped with its ridges on the exterior of the propodus and the dactyl, and a serrated edge on the inside of the immovable finger of the propodus, and a single domed tooth on the inside of the dactyl; the shape and setae on the 1st abdominal segment (viewed ventrally); the shape and setae of the posterior border; and the posterior border viewed in lateral profile relative to the posterior part of the carapace.

several long setae (Fig. 2A); cornea length is one third of total length of cornea plus peduncle (COL:COL + PED = 0.33:1).

Epistome: With small gap between dorsal point and front (Fig. 2A); short transverse ridge just below dorsal point and area above that is microscopically granulated; median area smooth and ventral projection is evenly microscopically granulated; sides and point of ventral projection flat with faintly finely serrated margins; ratio of width to length is 1: 2.63.

Third maxillipeds: Large, their greatest length is almost two thirds longer than the antero-lateral spine interspace (3MTL:ALSI = 1.56:1) and slightly longer than the length of the upper margin of the palm plus the moveable finger (3MTL:CHPLum + CHDL = 1.18:1); the length of the naked surface of the ischium is equal to the antero-lateral spine interspace (Fig. 2C); the length of the merus is slightly more than half that of the naked surface of the ischium (3MML:3MILns = 0.56:1); the upper portion of the merus appears smooth while the lower portion is granulated; the surface of the ischium is evenly granulated.

Abdomen: First segment has a projecting flange at the articulation with the carapace, comprising slightly less than half the total length of the first segment; first segment narrower at junction with second segment and successive segments increase in width to the fifth segment then decrease in width; the sixth segment is equal in length to the rounded seventh segment.

Cheliped: Slender with large spine on each ischium directed forwards and inwards (Fig. 2C). Lower outer margin of each merus with one small spine on distal half as long as the antero-lateral spine but not as stout, with two large spinules/granules below this; outer surface of merus heavily microscopically granulated above and below the median area which is sparsely granulated; inner surface of merus granulated with proximal end more heavily granulated; whole of merus appears faintly transversely furrowed. Wrist with tuft of setae on the inner surface (Fig. 2D), two fifths of the way down from the trigonal joint with the merus; wrist frontal edge has setae-filled groove defined by two granular ridges running from level of tuft to end of wrist; broad rugose ridge with microscopic granules forming short transverse rows along its length defines deep longitudinal groove along front of wrist; remaining dorsal surface of wrist evenly covered with microscopic granules and with very faint transverse furrows as in merus; length of wrist is almost as long as length of 1^{st} to 5^{th} abdominal segments. Palm with upper margin grooved; grooves filled with setae, as in wrist, but edge of ridges more serrated; a strong, scarcely granular ridge runs parallel to the front edge of the palm; another scarcely granular ridge runs obtusely from the moveable finger across to the lower palm edge near the junction with the wrist where it almost joins with a more strongly granular narrow ridge that runs longitudinally down the length of the palm and the immoveable finger; the concave area of the palm delineated by these ridges is rugose with transverse microscopically granular ridges and has the appearance of faint transverse furrows; another ridge with a line of short setae, near the lower edge of the palm, runs the length of the palm to become part of the lower border of the immoveable finger; this ridge is microscopically granular on the palm but becomes smooth down the length of the pollex; the lower border of the palm has a setae-lined microscopically granular ridge and the area between these two ridges is abundantly microscopically granulated; depth (width) of palm is almost equal to length of lower margin (CHPW:CHPLlm = 0.90:1). Immoveable finger surface is largely smooth and is defined on the lower border by a setae-lined groove and on the inner cutting edge by 9 irregular to rounded small teeth proximal to the palm. Immoveable finger length is slightly less than one and a half times the length of the lower border of the palm. Moveable finger has a broad, flat tooth on the cutting edge, appearing asymmetrically domed (longest side is towards palm), when viewed from the side and possessing several faint serrations at the base proximal to palm; a groove along the dorsal surface of the moveable finger is defined by two ridges running three quarters of the length of the finger, serrated to level of tooth and scarcely so thereafter; another smooth ridge runs from base of finger and forms a keel on the outer surface; moveable finger not quite as long as the wrist (CHCL: CHDL = 1.26:1) but longer than immoveable finger; the ratios of wrist and moveable finger with respect to the immoveable finger (CHCL: CHPOL) being 1.59:1.18: 1, respectively; moveable finger more curved than immoveable finger as in typical form; moveable finger tip meets immoveable finger slightly below the latter's tip.

Ambulatory limbs: Long and slender; merus of 4^{th} pair covered with microscopic granules denser near base; carpus microscopically granular and propodus smoother except for faint transverse furrows; dactyl short, broadly triangular in cross-section, setose, distinctly curved outwards on distal third and slightly flattened towards tip; ratio of merus length to dactyl length of 4^{th} walking leg is 1.54:1; dactyl slightly exceeds propodus of 4^{th} walking leg in length (4WLDL:4WLPL=1.26:1). Merus of 3^{rd} pair almost as long as 1^{st} to 5^{th} abdominal segments. Meri of ambulatory limbs have finely serrated ridges on antero-dorsal and ventral edges as well as postero-ventral edge; these ridges are particularly prominent and macroscopically granular on the meri of the 3^{rd} walking legs; the ventral regions of the meri are more densely granulated than in the M. longicarpus; central areas of the meri are weakly transversely furrowed as in cheliped merus. Carpi are microscopically granular and the propodi are smoother except for faint transverse furrows. Dactyls of 1^{st} to 3^{rd} walking legs are smooth with a central ridge on outer surface.

Gonopod: Comprises a flattened three-sided (cross-sectionally triangular) distally tapering shaft, with its ventral surface both convexly curved and parallel to the crab's sternum (Fig. 3C). The edges of the triangular shaft are keeled, and each face of the triangular form may have a longitudinal, length-parallel, broad and shallow runnel, the most prominent being on the dorsal-lateral face. The basal end of the gonopod has a mesial tapering flange. The shaft tapers in the distal half and curves at the tip (termed here the distal curvature). The tip is torsioned (or twisted) at almost 45° out of the plane of the dorsal orientation resulting in the point of the gonopod facing laterally outwards and parallel to the sternum. The distal curvature is a slightly overturned hook with a linear callosity on the ventral side adjacent to the sternum. A tuft of long setae arises from the rounded end of this latter structure. The lateral surface of the shaft below the distal curvature is spatuloid, *i.e.*, there is a spoon-like concavity on the shaft leading up to the inner curvature. The extreme distal tip of the gonopod has a pointed triangular chitinous structure. The distal extremity of the gonopod also is variably fringed by setae, dense enough to completely cover and conceal the chitinous structure. Lines of setae also may be sparsely distributed on the angular edges of the shaft, or within the length-parallel runnel. Gonopod length extends from 3rd to 6th segment with tip being visible just above end of sixth segment.

Colour: When alive, body is coloured sky blue dorsally, on the 3rd maxillipeds and on the abdominal segments; branchial regions paler with pinkish tinge; all limbs, including chelipeds are uniformly cream coloured, with no colour patches on the joints. Preserved specimens still retain some dark blue colouration on the dorsal surface and abdominal segments but otherwise are white except for small dark tips on the fingers. There is some colour variation with adult males from Broome having orange coloured limbs and setae and specimens from Monkey Mia, Shark Bay having salmon pink branchial regions. All crabs examined in the study area exhibited the characteristic of uniform colouration of limbs, and absence of colour patches on the limb joints.

Size: The largest adult male measured in this study was from Monkey Mia, Shark Bay, with a CL of 17.5 mm from the WAM C8038 collection dated 25th August 1960. The smallest adult male or sub-adolescent (as defined by blue colouration and participation in swarming) from Settlers Beach near Cossack, had a CL of 7.5 mm, representing a size range of 10.0 mm.

Variation: Large, older adult males have a more sculptured carapace, distinctly mounded cardiac hump and robust chelipeds and ambulatory limbs. The shape of the tooth on the moveable finger may vary with age from very asymmetric and incisor-like to a more rounded, domed profile. The number of teeth on the cutting edge of the immoveable finger is variable, with 7–9 observed in the paratypes. There is some slight variation in the shape of the front with lateral margins more or less convex and centre of median lobe more or less obtusely pointed. In juvenile males, the carapace is more globular, regional grooves less distinct, chelipeds slender with spine on merus poorly developed or absent, and tooth on moveable finger smaller, or absent; colour brown, becoming bluer at sub-adolescence. Sexual dimorphism occurs with females – they are smaller than males of same age, have no tooth on cheliped moveable finger, have obsolete spine on ischium, and their spine on the cheliped merus is reduced.

Summary of morphological description

Carapace visibly granular; rounded posterior border (viewed dorsally) projecting beyond abdomen; branchial regions uniformly granular, slightly inflated and overhanging base of ambulatory limbs; average carapace length 13 mm, CL:CW 1.21:1; antero-lateral spines prominent, recurved, broad, granular; prominent granular ridges from base of antero-lateral spine, one extending posteriorly to branchial regions, and another extending downwards to sub-hepatic regions; eyes medium, cornea not greatly wider than peduncle and one third total eye and peduncle length; front granulated with convexly curved lateral margins and obtusely pointed median lobe, margins are carinated and granular; 3rd maxillipeds granulated with merus slightly greater than half the length of the ischium naked surface; abdomen with first segment flanged at posterior articulation with carapace, 6th segment is equal in length to 7th segment; cheliped slender, visibly granulated, with well-defined grooves and granulated ridges; single forward-facing spine on cheliped ischium; single spine on merus outer margin; length of wrist is almost as long as length of 1st to 5th abdominal segments; palm with well-defined granular ridges; depth (width) of palm is almost equal to length of lower margin; immoveable finger length is slightly less than one and a half times the length of the lower border of the palm; moveable finger not quite as long as the wrist; prominent asymmetrical broad, domed, largely smooth tooth on cutting edge of moveable finger; merus of 3rd pair of walking legs almost as long as 1st to 5th abdominal segments; dactyl of 4th pair of walking legs short and distinctly curved along distal half.

Description of female allotype

Material examined: Allotype: female (CL 10.06 mm, CW 8.15 mm) (VCSRG KB12 swarm) King Bay, Dampier Archipelago, Western Australia, 20° 38' 16" S, 116° 45' 50" E (WGS84), coll. J. Unno, 24 Apr. 2003.

Carapace: Sub-globular and granulated, with projecting, rounded posterior border as in male; CL:CW ratio 1.22:1; anterior spines smaller but more heavily granulated than male holotype with a row of short bristles running along ridge to branchial regions and a tuft of long setae on short ridge to sub-hepatic region. Third maxillipeds as in male except ischium appears more granular and evenly covered with short bristles.

Cheliped: More slender than in male; carpus with longer setae on anterior margin; palm with ridges as in male; fingers slender and lacking tooth on moveable finger and ridges on immoveable finger.

Walking legs: More slender than in male; dactyl on 4th walking leg curved as in male.

Abdomen: Similar to male but more rounded in profile resulting in a greater body height (BH); male CL:BH ratio = 1.18:1; female CL:BH ratio = 1.11:1. The seventh abdominal segment is *circa* 10 % wider than in the male.

Gonopores: Located mesially on third sternal segment; small, simple dentoid spur projecting from end of third abdominal segment.

Colour: Allotype specimen is bluish-brown. Adult females in life show more colour variation than adult males with some females bright blue as in the males but many are brown or grey depending on stage of moulting.

Size range: Adult females are always smaller than males of the same age, being approximately three-quarters the size of their male counterparts.

Largest female: CW = 12.5 from Shark Bay near Carnarvon Racecourse.

Smallest female: CW = 7.1 from Settler's Beach, Cape Lambert.

Habitat

Low to medium energy wave-agitated environments with fine to medium (to coarse), sandy to slightly muddy sand substrates. Gently sloping intertidal shore zones including low gradient beaches, high to mid tidal sand flats, mid tidal shoals, tidal creek banks and tidal creek shoals. Usually in conjunction with a source of organic material such as mangroves or seagrass banks.

Behaviour

A benthic, cryptic species, generally inhabiting the substrate to a depth of 10–15 cm although crabs will rapidly move deeper if excavated. Females are more cryptic than males, rarely appearing on the surface. Subterranean feeding and emergence or re-entry activities by crabs at low tide produces mounds, tunnels, and rosettes of worked substrate on the tidal-flat surface, and exit holes. Large numbers of crabs (predominately adult males) may emerge at low tide to commence surface feeding and thus, although crabs are behaving individually, may have the appearance of an "army". Crabs turn sideways and burrow in a circular motion into the sand using the cheliped and ambulatory limbs, never the 3rd maxillipeds. Some crabs, if disturbed on the surface during feeding, will run with sand packed inside and extending the 3rd maxillipeds.

Distribution

Sub-tropical to tropical. Recorded on the mainland coast of Western Australia from Monkey Mia, Shark Bay 25° 47' 36" S, 113° 43' 18" E (WAM C8038) to One Arm Point, Dampier Peninsula 16° 26' 18" S, 123° 03' 42" E (WAM C39414). Also recorded within this latitudinal range from offshore islands such as Montebello Is (McNeil, 1926) and Legendre Is, Dampier Archipelago (WAM C39408). I have examined specimens of *Mictyris* from the Western Australian Museum holdings, collected further north than One Armed Point in Western Australia and from the Northern Territory region (north-west of Unwins Island, North Kimberley, WAM C19116, Lee Point, Darwin, WAM C39389, and West Woody Creek, Gove, NT, WAM C13033) and these specimens appear to be one species, diagnostically with two large spines on the inner merus of the cheliped, which does not accord with the characteristics of *M. occidentalis* or *M. longicarpus*. They may be the "Northern Territory" species referred to by McNeill (1926), and noted by Davie (2002) as being undescribed. No reliable records exist of soldier crab occurrence south of Shark Bay. McNeill (1926) cites a record of *Mictyris* from the Swan River in Perth by Miers in 1884 but this is highly unlikely due to the lack of suitable climate and habitat.

Etymology

The species name is derived from the Latin *occidentalis* meaning "of the West", alluding to the location of the species in Western Australia and distinguishing it from eastern Australian congeners.

Morphological comparison of *M. occidentalis* with *M. longicarpus* and *M. brevidactylus*

In describing *M. occidentalis*, emphasis has been placed on clearly distinguishing the new species from other described *Mictyris* species that may appear superficially similar, which may have adjoining distribution boundaries, and which have been taxonomically confused in the past, *i.e., M. longicarpus* and *M. brevidactylus. M. livingstonei* and *M. platycheles* have limited distributions on the east coast of Australia and, in addition, are quite dissimilar to *M. occidentalis, M. longicarpus* and *M. brevidactylus* in numerous morphological characters that have been well described in the literature (Milne Edwards 1852, McNeill 1926, Takeda 1978). *M. occidentalis* does exhibit some characters which appear similar to those ascribed to either *M. longicarpus* or *M. brevidactylus*, however, closer examination shows distinct differences. For example, both *M. longicarpus* and *M. occidentalis* have projecting carapace posterior borders when viewed dorsally, but are morphologically very different when viewed from a ventral or lateral aspect; also, *M. occidentalis* and *M. brevidactylus* have curved 4th walking leg dactyls, however, in the former, almost the whole length of the dactyl is curved while in the latter, the curve is mainly at the tip of the dactyl. Biometric data were useful in separating the new species from congeners, supporting the descriptive analysis.

The three *Mictyris* species of this study are systematically compared in all major morphological features in the text below and in Tables 4–6 and Figures 4–7. A summary of major morphological differences is presented in Table 7. The rationale for ordering the species along the x-axis in Figure 7 is based on the biogeographical arrangement of the data from the various Western Australian sampling sites which are ordered left to right latitudinally from Shark Bay in the south to the Broome region in the north (subtropical to tropical), effectively spaced in relation to their relative distance from each other. This logically would place data on *M. brevidactylus*, which geographically occurs in the Southeast Asian region, at least 1000 km further north of the Broome region, even further to the right on the x-axis, and the same distance from Broome that Shark Bay is from Broome to the south. In this framework, since *M. longicarpus* occurs along the eastern Australian coast at latitudes similar to Shark Bay in the south to Broome in the north, the occurrence of *M. longicarpus* on the axis of Figure 7 logically should be placed over the same interval as *M. occidentalis*. However, since it does not form part of a geographic (climatic) gradient, and occurs in a separate geographic location, *M. longicarpus* is placed on the far left of the x-axis. It is also placed to the far left to test the idea that *M. occidentalis* is intermediate between *M. longicarpus* and *M. brevidactylus*.

Detailed comparison of diagnostic characters

Body: There is a striking difference in body size between *M. longicarpus* and the other two species, the former being approximately 1.5 times the latter. *M. longicarpus* is generally 25–30 mm in carapace length, while *M. occidentalis* and *M. brevidactylus* are generally only 12–15 mm in carapace length. The largest *M. occidentalis* recorded in this study, from examining thousands of individuals along the Western Australian coast, were ten individuals of size *circa* 17 mm from Monkey Mia.

McNeill (1926) attributes the relatively small size of *M. longicarpus* var. *brevidactylus* (what is now generally considered to be *M. brevidactylus*) to general reduction in size of species in the tropical regions.

However, this does not explain the consistently greater size of the *M. longicarpus* specimens from Townsville, Queensland, a location which is definitively in a tropical region.

All three species examined in this study are sub-globular in body shape, with inflated branchial regions and truncated posterior borders. However, there is a difference between the three species in the degree of inflation of the branchial region in relation to the base of the walking legs: that of *M. longicarpus* does not overlap the base of the walking legs, that of *M. occidentalis* slightly overlaps, and that of *M. brevidactylus* distinctly overlaps, and thus the latter has the most globular shape. This trend is shown in Figure 7A where *M. occidentalis* is closer to *M. longicarpus* than *M. brevidactylus* in the CL:CW ratio.

M. brevidactylus appears to have the broadest gastric width (GW) of the three species, followed by *M. occidentalis* and then *M. longicarpus* which has the narrowest gastric region. This observation is substantiated by the antero-lateral spine interspace to posterior border width ratios (Fig. 7B). The posterior border of the carapace, as viewed dorsally, is significantly different in all species. *M. occidentalis* has the most noticeable posterior border which is a distinctly horizontally projecting and convexly rounded structure, densely fringed with long setae; *M. longicarpus* has a less projecting, downward-oriented, nearly straight border, densely fringed with short setae and *M. brevidactylus* has no projection and a straight-edged border with a very short fringe of setae (Figs. 4B, 6A and 7F).

Carapace and antero-lateral spines and ridges: *M. occidentalis* is distinctive in its carapace, having a visibly more granular carapace that is not smooth to the touch; the other two species have a less granular carapace. *M. brevidactylus* is more granular in the median area of the carapace than *M. longicarpus*. The branchial regions are differentially granulated in all the species, with *M. occidentalis* having evenly spaced, single macroscopic granules, *M. brevidactylus* having macroscopic granular rugae and *M. longicarpus* having microscopic closely set granules. The antero-lateral spines and associated ridges (posteriorly to branchial regions and downwards to sub-hepatic regions) are diagnostic in *M. occidentalis* as they are visibly granular and prominent (Fig. 5A).

In *M. longicarpus*, the antero-lateral spines are prominent but have few granules at their bases and the ridges are ill-defined and only microscopically granular, while *M. brevidactylus* has less prominent and granular antero-lateral spines and the associated ridges are significantly less granulose (Figs. 5B and 5C).

Front and eyes: *M. longicarpus* is distinctive in having large globulose eyes on stout peduncles (Fig. 5B) and a narrow-appearing front that has nearly straight lateral margins with the front width being equal to front length. In contrast, *M. occidentalis* and *M. brevidactylus* have smaller eyes, but similar in size to each other. However, *M. occidentalis* has a narrower front (front length is four fifths front width) than *M. brevidactylus*. *M. brevidactylus* has the broadest front (front length is two thirds front width) of the three species (Fig. 7D). *M. occidentalis* exhibits greater granularity in its front than the other two species, especially on the epigastric ridges and the front margins (Fig. 4A).

Third maxillipeds: All three species are divergent in the relative proportions of the 3rd maxilliped merus and ischium, *i.e.*, the length of the merus in relation to the length of the naked surface of the ischium. The merus is slightly greater than half the length of the naked surface of the ischium in *M. occidentalis*, equal in *M. brevidactylus* and slightly less than half in *M. longicarpus*. The 3rd maxilliped is also macroscopically granulated in *M. occidentalis* and microscopically granulated in *M. longicarpus* and *M. brevidactylus*.

Abdomen: The size and morphology of the first abdominal segments of all three species are different (Figs. 5D–5F). Since they underlie the posterior border, the differences of the first abdominal segments reflect the markedly differing posterior carapace borders of the three species. All the species have an upwards slope in the posterior part of this first abdominal segment. However, in the posterior part towards the carapace border, *M. occidentalis* has a broad (almost half the length of the first segment) flat flange or platform projecting more horizontally outwards than downwards (Fig. 5D). The carapace also projects outwards more than downwards to meet the abdominal segment with a minor vertical overhang (Fig. 3C). In *M. longicarpus*, on the other hand, the first abdominal segment slopes linearly upwards for the entire length of the segment, without a distinct platform, to join the carapace; the lower portion of the carapace forms a vertically-long overhang, projecting slightly out and more vertically downwards to connect with the first abdominal segment (Fig. 5E). *M. brevidactylus* has a first abdominal segment with a short, strongly curved upward slope that meets the carapace which has a minuscule overhang (Fig. 5F).

Chelipeds: *M. occidentalis* differs in cheliped morphology from the other two *Mictyris* species in five aspects: 1. a greater degree of granulation on the outer surface of the wrist and the inner margins of the merus; 2. the length of the wrist is shorter than *M. longicarpus* (*M. longicarpus* is well-named), but longer than *M. brevidactylus*; 3. the width of the wrist is more slender than both species (Fig. 7E); 4. the palm is less wide; and 5. the length of the moveable finger is shorter. Of the three species, the structure of the cheliped of *M. occidentalis* most resembles that of *M. longicarpus* in the proportions of the immoveable finger, (Table 4) and the shape of the tooth on the moveable finger. While *M. longicarpus* is similar to *M. brevidactylus* in three of their cheliped ratios (1. the cheliped width is twice the wrist length; 2. the moveable finger is almost equal to the length of the wrist; and 3. the width of the palm is equal to the length of the lower palm border), the cheliped ratios of *M. occidentalis* are dissimilar in all respects to those of *M. brevidactylus*. Significant ratios of cheliped features are presented in Table 4 and Figure 7E and chelipeds of the three species are illustrated in Figure 4D. In adult males, the tooth on the moveable finger is asymmetrically domed in *M. occidentalis*, conical in *M. longicarpus* and asymmetrically serrated in *M. brevidactylus* (Fig. 4D).

Walking legs: All three species show similarity in the slenderness of the walking legs. The most useful

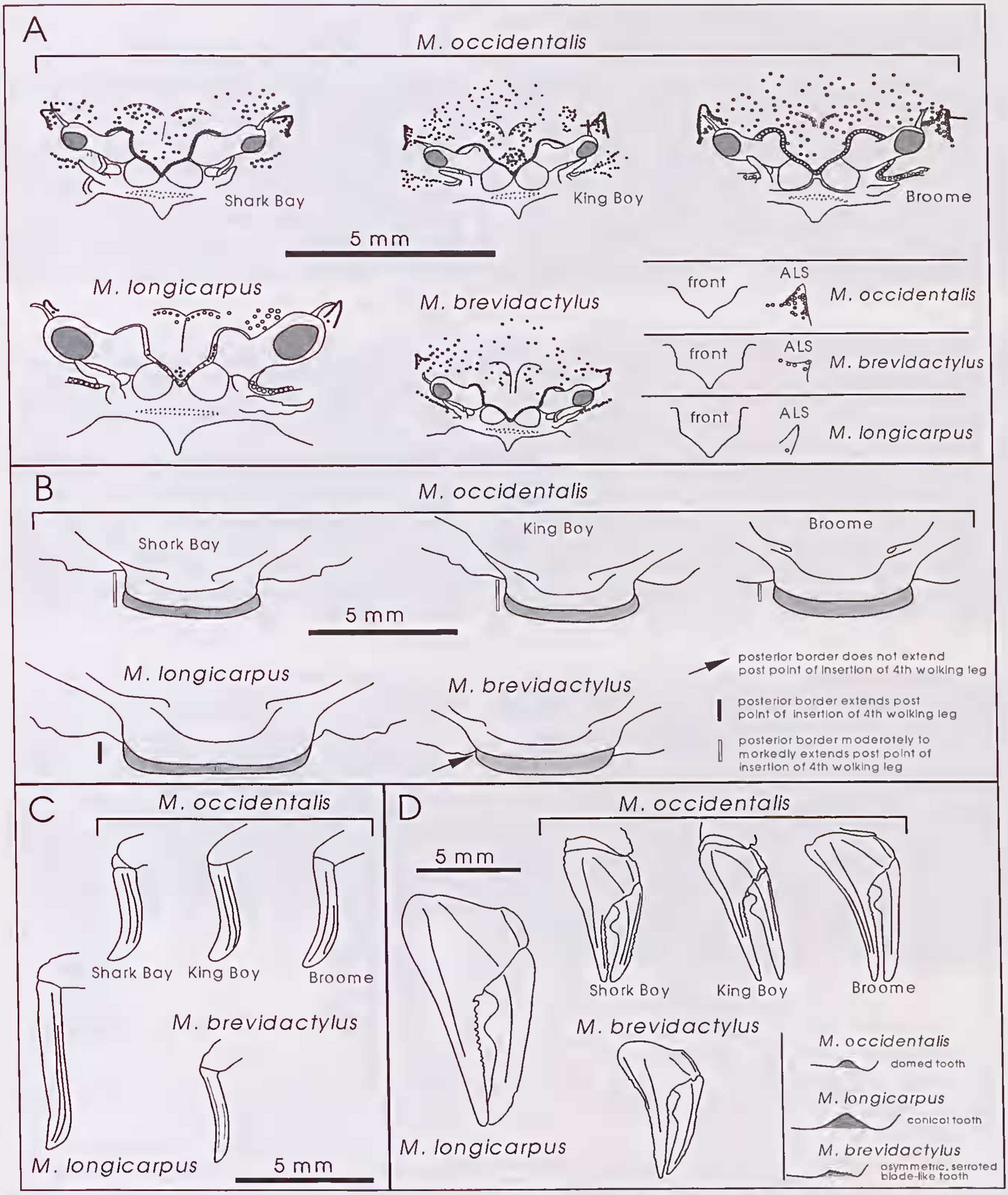

Figure 4. Comparative anatomy of *Mictyris occidentalis*, *M. longicarpus*, and *M. brevidactylus*. In each diagram, for *M. occidentalis*, individuals from Shark Bay, King Bay (Dampier Archipelago), and Broome are illustrated to show intra-species and geographic variation. A. The anterior front view of the three species showing: shape of front and the extent of granulation along its edge; eyes and relative size of cornea and peduncle; antero-lateral spine and the extent of its granulation; and the extent of granulation of the dorsal carapace; inset illustrates the differences between the three species by focusing on the shape of the front, and the orientation and extent of granulation of the antero-lateral spine. B. Shape of the posterior border, and extent that the posterior border extends past the point of insertion of the 4th walking leg. C. Dactyl of the 4th walking leg; *M. occidentalis* is relatively short and curved, *M. longicarpus* is relatively long, and *M. brevidactylus* is short and curved but more slender than that of *M. occidentalis*. D. Chelipeds: *M. occidentalis* has a serrated edge on the inside of the immovable finger of the propodus, and a single domed tooth on the inside of the dactyl; *M. longicarpus* also has a serrated edge on the inner surface of the immovable finger of the propodus, and a single conical tooth on the inside of the dactyl; *M. brevidactylus* lacks a serrated edge on the inside of the immovable finger of the propodus, and has an asymmetrical blade-like, triangular single tooth on the inside of the dactyl that is serrated on its proximal edge and smooth on its distal edge; inset diagrammatically illustrates the differences in the tooth on the inside of the dactyl for the three species.

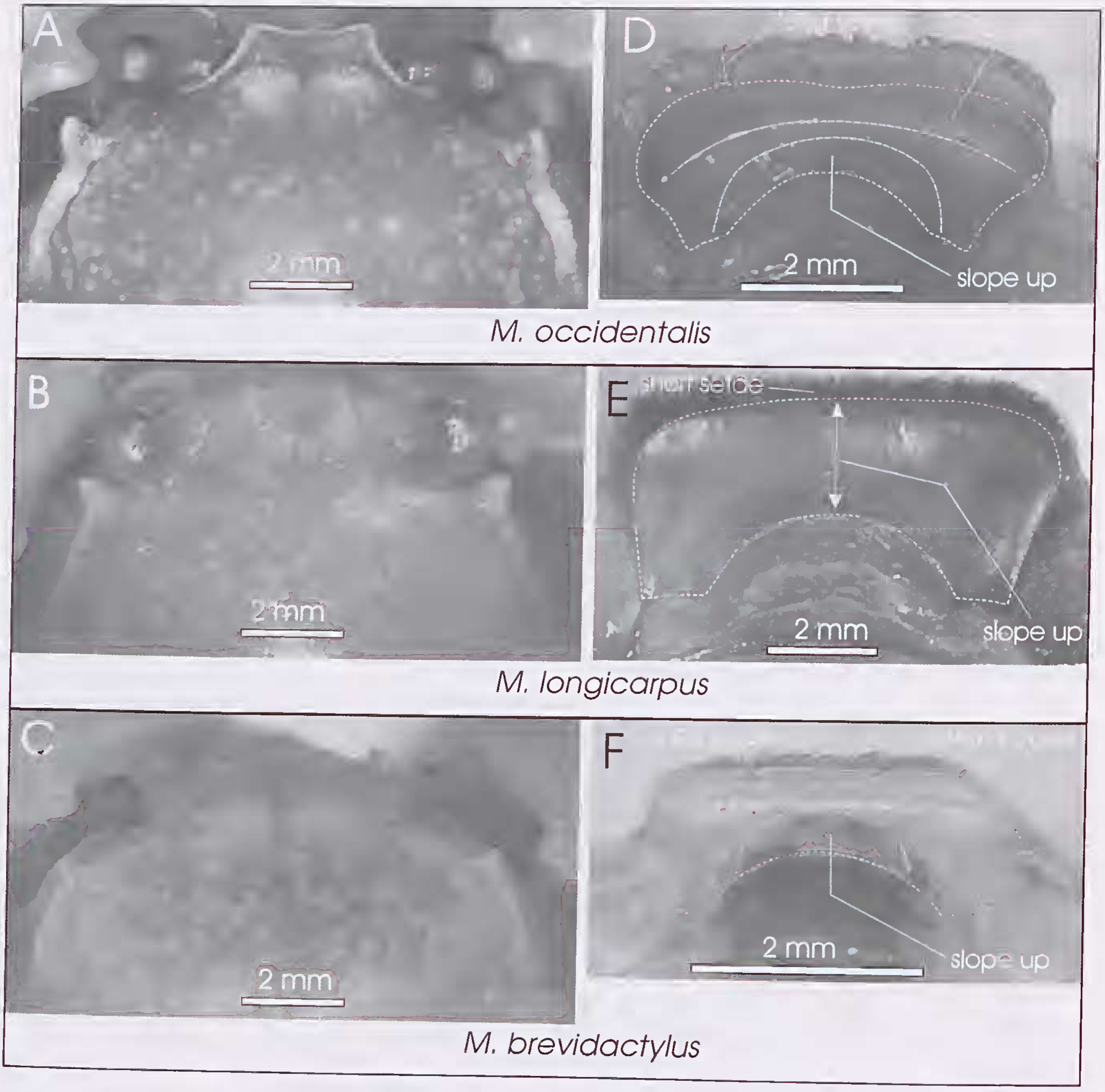

Figure 5. Comparative anatomy of *Mictyris occidentalis*, *M. longicarpus*, and *M. brevidactylus*. A–C. Dorsal view of carapace front for each of the species showing the differences in granulation of the carapace, granulation of the front, the length and thickness of the peduncle, the size of the eyes, and the variation in granulation of the antero-lateral spines. D–F. Ventral view of 1st abdominal segment showing the variation in its plan shape between the species, the extent that depressions and ridges comprise the form, and the extent of development of setae along the posterior margin.

diagnostic features of the legs for comparative purposes are the dactyl of the 4th walking leg with respect to its shape and length in relation to the propodus of the same limb, and the merus of the 3rd walking leg with respect to its total length. *M. longicarpus* is easily distinguished from the other species, with its long, relatively straight 4th WL dactyl (4WLDL: 4WLML = 1.22: 1). *M. occidentalis* and *M. brevidactylus* both have short, curved 4th WL dactyls, however, *M. brevidactylus* is slightly the shorter (1.65 times the merus length as opposed to 1.50 times in *M. occidentalis*) and the dactyl of *M. occidentalis* has a greater curvature (Fig. 4C and Fig. 7C). *M. occidentalis* and *M. brevidactylus* are similar in having the length of the 3rd WL merus equal the length of the 1st to 5th abdominal segments, while that of *M. longicarpus* equals the 1st to 6th abdominal segments.

Gonopods: The gonopods of *Mictyris* examined in this study, though broadly similar, show some discernible differences between the species. A gonopod of *M. occidentalis* is illustrated in Figure 2F. The key features that help to distinguish between the three species are: beginning point of torsion on shaft (viewed

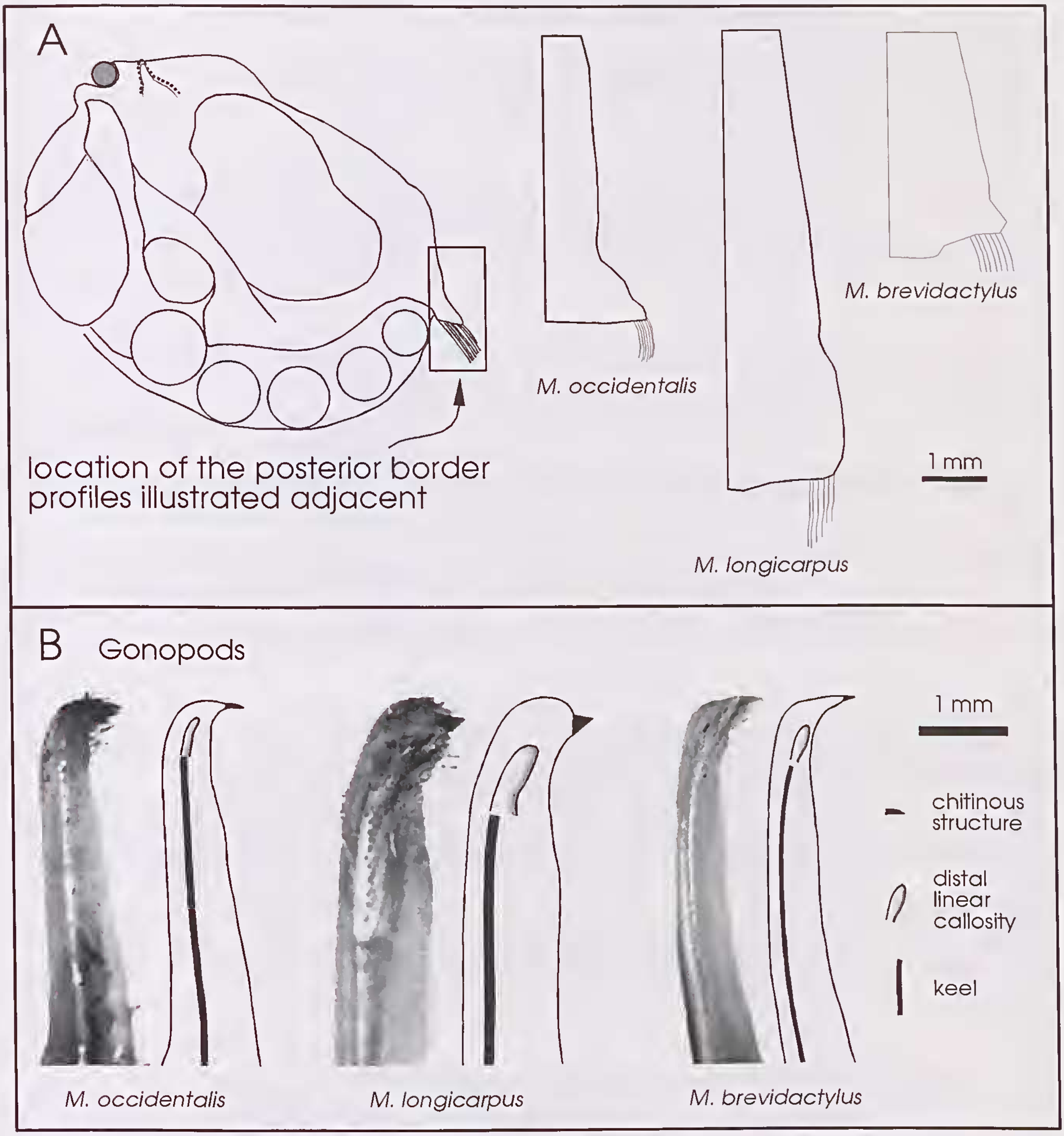

Figure 6. Comparative anatomy of *Mictyris occidentalis, M. longicarpus,* and *M. brevidactylus.* A. Variation in the profile shape of the posterior border. Cross section of carapace shows where the detailed drawings of the posterior border are located. Individual drawing shows a prominent sloping platform for the posterior border for *M. occidentalis,* a steep, relatively high protrusion for *M. longicarpus,* and a short sloping platform for *M. brevidactylus.* B. Variation in gonopod morphology between the three species.

on the anterior surface); extent of curvature of the tip of the shaft; length of the chitinous structure relative to the diameter of the distal end of the shaft; extent of development of the concavity of the spatuloid shape; the extent of development of the keel; and the development of the longitudinal furrow. Setae and their extent of development did not appear to be species-diagnostic except that *M. brevidactylus* was sparsely setose on the shaft. A comparison of the three species is provided in Table 5 and Figure 6B.

Of the three congeners, the gonopod of *M. occidentalis* exhibits the greatest degree of torsion with the twist beginning at the midpoint of the shaft rather than higher towards the distal end as in the other species. In general appearance, the gonopod of *M. occidentalis* has greater similarity with *M. brevidactylus* than with

Table 4

Comparison of cheliped morphology

Cheliped ratios	*M. occidentalis*	*M. longicarpus*	*M. brevidactylus*	Explanation of ratios
CHCL:CHCW:	2.49:1	2.01:1	1.99:1	wrist length is 2 ½ times wrist width in *M. occidentalis* and ~ 2 times in *M. longicarpus* & *M. brevidactylus*
CHPOL:CHPLlm	1.45:1	1.42:1	1.00:1	immoveable finger is ~ 1 ½ times length of palm lower margin in *M. occidentalis* & *M. longicarpus* but equal in *M. brevidactylus*
CHDL:CHCL	0.82:1	0.90:1	0.94:1	moveable finger much shorter than wrist in *M. occidentalis*, slightly shorter in *M. longicarpus* and almost equal in *M. brevidactylus*
CHPOL:CHCL	0.71:1	0.75:1	0.58:1	immoveable finger is ~ ¾ length of wrist in *M. occidentalis* & *M. longicarpus* but ~ $^2/_3$ in *M. brevidactylus*
CHPW:CHPLlm	0.80:1	0.90:1	0.91:1	palm width < length of palm lower margin in *M. occidentalis* and almost equal in *M. longicarpus* & *M. brevidactylus*
CHPW:CHPOL	0.64:1	0.66:1	0.75:1	palm width is $^2/_3$ length of immoveable finger in *M. occidentalis.* & *M. longicarpus* but ¾ in *M. brevidactylus*
CHCL:ALSI	1.30:1	1.51:1	1.15:1	wrist length is 1 $^1/_3$ times antero-lateral spine interspace in *M. occidentalis,* 1 ½ times in *longicarpus* and almost equal in *M. brevidactylus*

Table 5

Comparison of gonopod morphology

Gonopod feature	*M. occidentalis*	*M. longicarpus*	*M. brevidactylus*
torsion of shaft	begins at midpoint of shaft	begins just before curve of tip	begins at three-quarters of length of shaft
curvature of the tip of the shaft	curved with slightly extended tip	curved with short hooked tip	curved with distinctly extended tip
description of the chitinous structure	long and thin	long and thick	short and thin
location of the chitinous structure	in line with the apex of curvature of the shaft	below the apex of the curvature of the shaft	in line with the apex of curvature of the shaft
concavity of the spatuloid shape	well developed	moderately developed	weakly developed
keels	prominent	prominent	present, but weakly developed
furrows	prominent	prominent	weak
setae	along shaft and well developed at tip	along shaft and well developed at tip	generally sparse along shaft, but well developed at tip
length	from 3rd abdominal segment to just above 6th segment (visible)	from 3rd abdominal segment to below top of 6th segment (not always visible)	from 3rd abdominal segment to just above 6th abdominal segment (visible)

Table 6

Comparison of gonopore morphology

Gonopore feature	*M. occidentalis*	*M. longicarpus*	*M. brevidactylus*
size of spur	small	large	almost obsolescent
shape of spur	simple, dentoid, blunt point	multifurcate, dentoid, blunt point	simple, sharp point
setae	sparse fringe	dense short fringe at end	very sparse

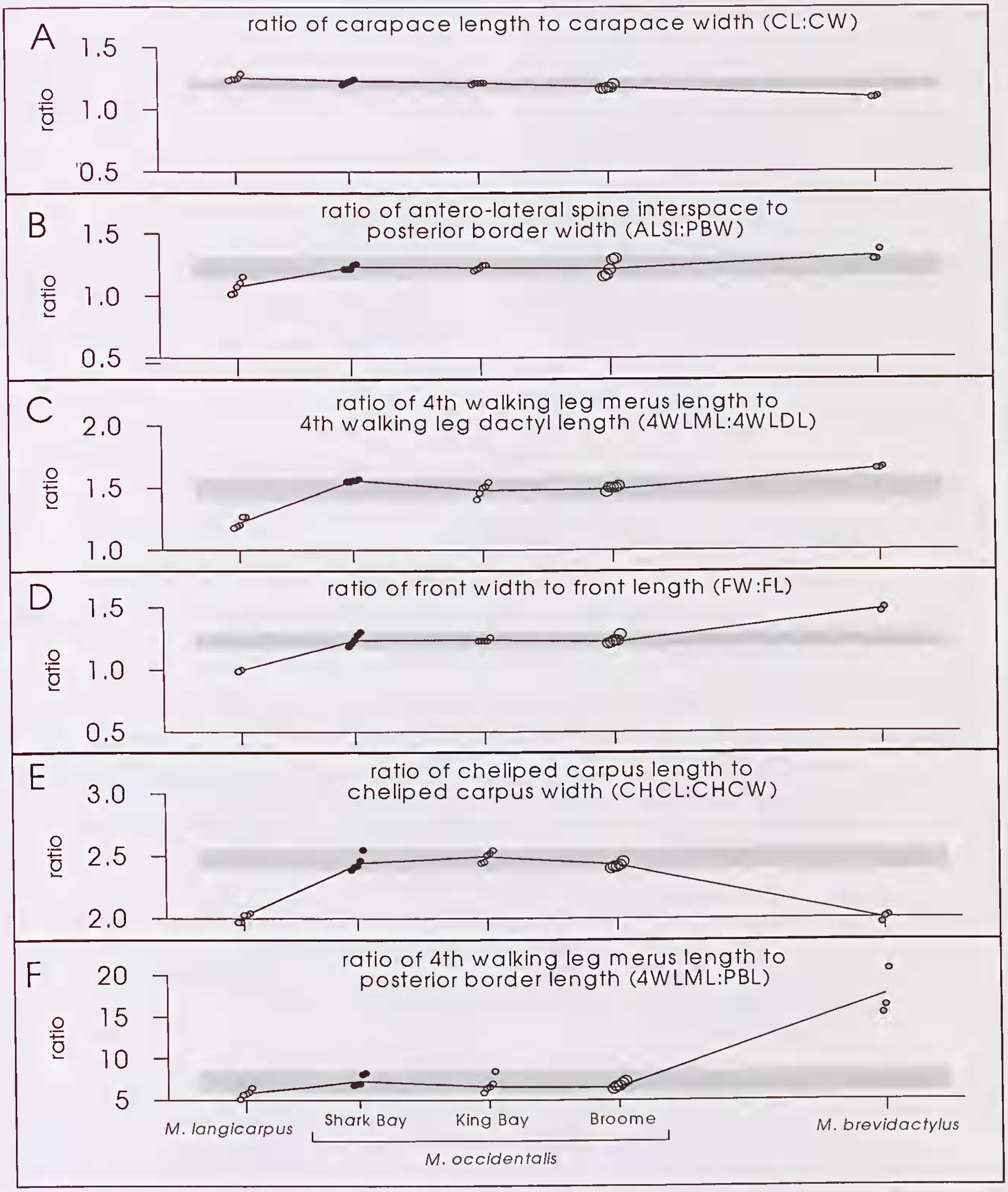

Figure 7. Ratio of various anatomical features of *Mictyris occidentalis, M. longicarpus,* and *M. brevidactylus.* The grey band in each graph shows the variation in value of the ratio for the holotype and the 14 paratypes of *M. occidentalis*, based on three latitudinally widespread sites, with 5 male crabs from each site. A. The ratio of carapace length to carapace width which shows *M. longicarpus* and *M. brevidactylus* are just outside the degree of variation of the ratio for *M. occidentalis.* B. The ratio of antero-lateral spine interspace to posterior border width with *M. longicarpus* and *M. brevidactylus* just outside the degree of variation of the ratio for *M. occidentalis,* and with *M. occidentalis* intermediate in value to those of the other two species. C. The ratio of 4th walking leg merus length to 4th walking leg dactyl length, with *M. longicarpus* and *M. brevidactylus* definitively outside the degree of variation of the ratio for *M. occidentalis,* but with *M. occidentalis* intermediate in value to those of the other two species. D. The ratio of front width to front length with *M. longicarpus* and *M. brevidactylus* definitively outside the degree of variation of the ratio for *M. occidentalis,* but again with *M. occidentalis* intermediate in value to those of the other two species. E. The ratio of cheliped carpus length to cheliped carpus width with *M. longicarpus* and *M. brevidactylus* definitively outside the degree of variation of the ratio for *M. occidentalis,* but with *M. occidentalis* not intermediate in value to those of the other two species. F. The ratio of 4th walking leg merus length to posterior border length; *M. longicarpus* is similar to *M. occidentalis,* and *M. brevidactylus* definitively outside the degree of variation of the ratio for *M. occidentalis.*

M. longicarpus in that the head of the distal curve is longer, although not to the extent of *M. brevidactylus*. However, the shaft has more affinity to *M. longicarpus* with prominent keels and furrows.

A summary of the major morphological similarities and differences of the three *Mictyris* species considered in this study is presented in Table 7 below.

Gonopores: Gonopores of the three species share the same feature common to the genus of being a cavity overhung on the mesial side with a projection or spur formed from the end of the 3rd abdominal segment. The greatest variation in the gonopores is in size and complexity of the spur ranging from an almost obsolescent, pointed spur in *M. brevidactylus*, to a small, blunt spur in *M. occidentalis*, to a large, complex spur in *M. longicarpus* (Table 6).

Species Key

A key to distinguish the adult males of the five described species of *Mictyris* Latreille, 1806 including the three species considered in this paper, is presented below:

Key to *Mictyris* Latreille, 1806

A1. Posterior border of carapace conspicuously produced and overlapping abdomen

B1. Carapace macroscopically granular, antero-lateral spines and ridges prominent, and strongly granular, branchial regions overlapping base of legs, dactyl of 4th WL distinctly curved along distal third, average size, 12 mm CL .... *occidentalis*

Table 7

Summary of major differences between *Mictyris* species

Species Character	*M. occidentalis*	*M. longicarpus*	*M. brevidactylus*
carapace	macroscopically granular, not smooth to touch	appears smooth, microscopically granular, smooth to touch	sparsely granulated, not entirely smooth to touch
branchial regions	moderately inflated, slightly overlapping base of walking legs; macroscopically granular with single granules	slightly inflated, not overlapping base of walking legs; microscopically granular	distinctly inflated, overlapping base of walking legs; macroscopically granular with rugae
posterior border antero-lateral spines and ridges	distinctly projecting and convex broad and granular, recurved, oriented outwards more than upwards; prominent granular ridge running backwards to branchial region and another short, strongly granular ridge downwards to sub-hepatic region	projecting, slightly sinusoidal prominent, recurved, oriented outwards more than upwards; smooth except for sparse granules at base; ill-defined ridge running backwards to branchial regions and another short, microscopically granular ridge downwards to sub-hepatic region	not projecting, straight prominent, recurved, oriented upwards more than outward; sparsely granular, sparsely granular ridge running backwards to branchial regions and another short, microscopically granular ridge downwards to sub-hepatic region
front	broad, convexly curving laterally	narrow, straight laterally	very broad, straight laterally
eyes	medium, globular	large and globulose; stout peduncle	small, globular
third maxillipeds	lower part of merus and all of ischium heavily granulated; length of merus slightly more than half that of naked surface of ischium	microscopically granulated; length of merus less than half that of naked surface of ischium	microscopically granulated; length of merus half that of naked surface of ischium
Abdomen Chelipeds	7th segment equal to 6th wrist and palm slightly more slender; front surface of wrist and margins of merus visibly granulated; narrower palm and shorter moveable finger; fingers tapering at ends; slightly asymmetrical domed tooth on moveable finger with faint serrations on side proximal to palm	7th segment longer than 6th Wrist and outer surface of palm smooth; fingers long and robust; large conical tooth on moveable finger	7th segment equal to 6th carpus and palm wide; fingers short (immoveable finger almost equal length of lower palm) and sturdy; broad, serrated asymmetrical tooth on moveable finger
walking legs	merus of 3rd pair as long as 1st to 5th abdominal segments; dactyl of 4th walking leg short, setose and distinctly curved over distal third	merus of 3rd pair as long as 1st to 6th abdominal segments; dactyl of 4th walking leg long and slightly curved at tip	merus of 3rd pair as long as 1st to 5th abdominal segments; dactyl of 4th walking leg short and distinctly curved at tip
gonopods	sturdy shaft, slender tip stout, keeled, long distal curve, prominent chitinous tip	stout, short distal curve, prominent chitinous tip	slender, very long distal curve, short chitinous tip
gonopores	small, simple spur	large, setose, multifurcate spur	almost obsolete simple spur

B2. Carapace not macroscopically granular, appearing smooth; branchial regions not overlapping base of walking legs; antero-lateral spines recurved, without strongly granular ridges, dactyl of 4th WL straight with slightly curved tip; large globulose eyes, large size, 20–30 mm CL .... *longicarpus*

A2. Posterior border of carapace produced but not overlapping abdomen; carapace covered with whitish tubercules, branchial regions dorsally swollen, average size 16 mm CL .... *platycheles*

A3. Posterior border of carapace not conspicuously produced

B1. Prominent broad serrated tooth on cutting edge of moveable finger; granular ridge from antero-lateral spine posteriorly to branchial region, average size 12 mm CL .... *brevidactylus*

B2. Obsolete tooth on cutting edge of moveable finger; no ridge from antero-lateral spine posteriorly to branchial region, small eyes, average size, 11 mm CL .... *livingstonei*

Discussion and conclusions

Qualitative and biometric data point to the Western Australian form of *Mictyris* as a new species. It is morphologically distinct, and can be readily distinguished from *M. longicarpus* by its smaller size, rounded and projecting posterior border, more granular carapace, more inflated branchial regions, prominent ridges extending from the antero-lateral spines, broader front, and short, curved dactyl on the 4th walking leg; and from *M. brevidactylus* by its projecting posterior border, more granular carapace, less inflated branchial regions, prominent ridges extending from the antero-lateral spines, narrower front and domed tooth on moveable finger of cheliped.

The ratios of morphological features of *M. longicarpus* and *M. brevidactylus* determined in this study corroborate the ratios for these species determined in earlier studies by Latreille (1806), Stimpson (1858), and McNeill (1926). Many of the ratios appear to be species-diagnostic (*viz.*, the ratios of carapace length to carapace width, antero-lateral spine interspace to posterior border width, front width to front length, and 4th walking leg merus length to dactyl length) and are significantly different between all three species. Additionally, *M. occidentalis* is clearly distinguished by the ratio of cheliped carpus length to cheliped carpus width, while the ratio of the merus length of the 4th walking leg to the posterior border length discriminates *M. brevidactylus* from the others (Fig. 7).

Some authors, (e.g., McNeill 1926), have considered the Western Australian form of *Mictyris* (*M. occidentalis* of this paper) to be a morphological intermediate between *M. longicarpus* and *M. brevidactylus*, and to test this idea, ratio data are presented in graphical form (Fig. 7) with data on *M. occidentalis* placed on the x-axis between the two congeners. Placement of the reduced data of ratios in this order in Figure 7 illustrates some significant patterns: for the ratios of carapace length to carapace width (Fig. 7A), the antero-lateral spine interspace to posterior border width (Fig. 7B), the 4th walking leg merus length to 4th walking leg dactyl length (Fig. 7C), and the front width to front length (Fig. 7D), *M. occidentalis* indeed appears to be intermediate between *M. longicarpus* and *M. brevidactylus*. However, for the ratios of cheliped carpus length to cheliped carpus width (Fig. 7E) and 4th walking leg merus length to posterior border length (Fig. 7F), *M. occidentalis* does not appear to be intermediate between *M. longicarpus* and *M. brevidactylus*. Similarly, other morphological features of the three *Mictyris* species do not support the idea that *M. occidentalis* is an intermediate between *M. longicarpus* and *M. brevidactylus*. These include, for instance, some of the morphological features of the gonopods (Table 5), as well as the ratio of the cheliped carpus length to cheliped carpus width, the ratio of the 4th walking leg merus to the posterior border length the shape of the posterior border, the shape of the 1st abdominal segment, and the degree of granularity of the carapace, the morphology of the antero-lateral spines, the shape of the front, and the granularity of the 3rd maxilliped.

In summary, while *M. occidentalis* shows some morphological similarity to *M. longicarpus*, and another set of similarities to *M. brevidactylus*, it has some of its own unique features. I consider it not to be an intermediate between *M. longicarpus* and *M. brevidactylus*.

The focus on comparing the morphology of the three species in this study has provided interesting information as to where the major variations in the characters of the genus occurs. These characters are: the arrangement of the carapace posterior border-first abdominal segment interface; the degree of inflation of the branchial region; the extent of granulation on the carapace; the form and granulation of the antero-lateral spine; the prominence of the branchial and sub-hepatic ridges extending from the antero-lateral spines; the shape and size of the tooth on the moveable finger; and the shape and size of the dactyl of the 4th walking leg. They appear to be the characters that consistently vary, though in different forms, from species to species. Of these, I consider that the arrangement of the carapace posterior border - first abdominal segment interface to be the most significant, and hence it is used as the first morphological criterion in the key to differentiate the species.

On the other hand, there are numerous other morphological features that do not vary markedly between species. Setting aside the tooth on the moveable finger, the shape of the chelipeds and the general pattern of the cheliped ridges and grooves appear to be relatively consistent unlike the major cheliped of the Ocypodid crab *Uca* which can vary greatly in form between species (Crane 1975; George & Jones 1982). Similarly, the general structure of the abdominal segments (except for the 1st segment), and the 1st to 3rd walking legs seem to be similar between the three *Mictyris* species of this study. As such, these features are not afforded significant status in differentiating between the species.

In terms of biogeography and regional species variation, the graphs of ratios of morphological features in Figure 7 highlight some interesting patterns. While there appear to be trends in ratios between the three congener species, as discussed earlier, there is a relative consistency in results for *M. occidentalis* for five ratios across a latitudinal spread of 17°S to 25°S (a distance of *circa* 1000 km), supporting observational data for a monospecific distribution from Shark Bay to Broome, and indicating for most of the morphological features, little variation across the biogeographic range of the species. As such, any morphological deviation of *M. occidentalis* from the other congeners becomes significant. The nearest occurrence of a described congener to *M. occidentalis* is *M. brevidactylus* and the morphological features for *M. occidentalis* and *M. brevidactylus* reflected in the ratios of Figure 7D–7F are relatively consistent for *M. occidentalis* over its geographic range, but definitively different for *M. brevidactylus* over the same geographic distance, thus corroborating that there are two separate forms.

Even putting aside their reproductive morphological differences, given the fact that populations of *M. brevidactylus* are some 1000 km further north of any *M. occidentalis* populations, and that the nearest occurrence of *M. longicarpus* is several thousand kilometres to the east in Queensland, these three congeners, occurring in separate, non-overlapping geographic areas, clearly are unable to cross-breed, and are therefore allopatric. In this context, *M. occidentalis,* is geographically limited to the northwest coast of Western Australia and hence is endemic.

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